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Influence of Topography on Cumulative Pollen Flow of Fourwing Saltbush

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Abstract—The influence of environmental heterogeneity on cumulative pollen flow is examined using fourwing saltbush (*Atriplex canescens*) growing on steep slopes and on alluvium at the base of the slope as a model system. Both the gender of the pollen donor (male or hermaphrodite) and the topography influence pollen dispersal. Additionally, the efficiency of pollen dispersal (the number of pollen grains dispersed to a given distance per unit of plant volume) is enhanced when plants grow on slopes. Plants become less efficient at dispersing pollen as they become larger.

Keywords: *Atriplex canescens*, gender, adaptation, fitness, pollination, wind, hermaphroditism, sex differences

Pollen dispersal has received considerable attention for insect-pollinated plants. Far less is known about the dispersal of pollen from wind-pollinated plants. Faegri and Van der Pijl (1971) as well as other researchers have noted that pollen of wind-pollinated species may travel long distances. The relative numbers of pollen grains at various distances from individual plants has received little attention. Thus, we know little about potential gene flow in wind-pollinated species. Nor do we understand whether wind-pollinated plants become increasingly fit as they become larger. Because wind-pollinated plants tend to dominate arid environments with uneven topography, we decided to investigate the influence of topography on pollen dispersal. This report provides data on pollen movement. It is a companion to Freeman and others (1993). That paper includes other fitness measures and describes the study more completely.

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METHODS

Fourwing saltbush (*Atriplex canescens*) is an anemophilous (wind-pollinated) evergreen chenopod shrub of the desert region of Western North America (Blauer and others 1976; Freeman and McArthur 1989; Wagner and Aldon 1978). Populations of fourwing saltbush occur on steep, dry slopes and on the deeper, moister, more fertile alluvium at the base of the slopes (Dunford 1984; Hall and Clements 1923; Stutz and Sanderson 1979). Populations of fourwing saltbush are subdioecious, containing staminate (male) and pistillate (female) individuals, as well as individuals with a mixture of staminate and pistillate flowers. The majority of plants containing a mixture of staminate and pistillate flowers may also produce perfect flowers, flowers with stamens and a pistil (Freeman and McArthur 1989). Since these individuals are not strictly monoecious, they will be referred to as hermaphrodites. The relative proportion of staminate and pistillate flowers produced by these individuals varies with time and may change in response to stress (Barrow 1987; Freeman and McArthur 1989; McArthur 1977; McArthur and Freeman 1982; McArthur and others 1992; Pendleton and others 1992; Stutz and others 1975).

STUDY SITE

The study site was in Kingston Canyon, Piute County, UT. It included the steep canyon slopes of the main and side canyons (slope sites) as well as the alluvium at the base of the slopes (alluvial sites) (fig. 1, see Freeman and others [1993] for physical and biological characteristics of the sites).

Figure 1—Kingston Canyon study site: (A) steep canyon slope; (B) alluvium. Fourwing saltbush grows on both sites.

Pollen dispersal was measured along the four cardinal axes. Twenty-four pollen donors (six males and six hermaphrodites on the slope, and six males and six hermaphrodites on the alluvium) were randomly chosen for this study. Competing pollen donors within 100 m were removed. Since mature males of fourwing saltbush produce more than 1 x 10^7 anthers per plant (McArthur and others 1992), emasculating competing pollen donors was untenable. Pollen traps (microscope slides coated with petroleum jelly fixed on sticks 0.7 m high) were placed at 3-m intervals for 30 m per axis per plant studied. Pollen traps were in place before anthesis (blooming). They were changed weekly during the 4-week flowering period. The number of dispersed pollen grains was estimated by counting the number of pollen grains in 10 (1-mm^2) fields of view using a compound microscope. Pollen dispersal along each of the cardinal axes was analyzed separately using an analysis of covariance with distance as the covariate. Orthogonal contrasts and *t* tests compared the effects of slope and alluvium. Regression analysis was used to measure the effect of increasing plant size on pollen (Norusis 1988; Zar 1984).

Since plants growing on the slope are in a harsher environment than those growing on the moister, more fertile alluvium, plants on the slope will always be smaller than mature plants on the alluvium. Since they are smaller, they should disperse fewer pollen grains (Freeman and others, 1993). We also examined the pollen flow corrected for the size of the plant. The size correction was made by computing the volume of the donor plant and dividing the number of pollen grains dispersed to a given distance by the volume of the dispersing plant. Plant volume was computed twice, first by treating the plant as a sphere, and then by treating it as a cylinder. For these calculations, we used half the crown diameter as the radius. We averaged the two estimates, since the shape of fourwing saltbush is between a cylinder and a sphere.

RESULTS

In figures 2 through 5 we plotted the mean number of pollen grains dispersed to a given distance in a given direction for males and hermaphrodites growing on the slope versus those on the alluvium. The data presented are summed over all four collection dates, and represent the total number of pollen grains/mm^2 of the pollen trap's surface area.

Males disperse significantly more pollen than hermaphrodites ($F_{1,720} = 28.13$, $P < 0.001$). Plants growing on the alluvium disperse more pollen than plants on the slope ($F_{1,720} = 28.00$, $P < 0.001$). Topographic position influenced pollen dispersal by males and hermaphrodites differently. The relative decline in pollen dispersal from the alluvium to the slope was much greater for hermaphrodites ($F_{1,720} = 7.67$, $P < 0.01$). Hermaphrodites on the slope dispersed the fewest number of pollen grains, particularly along the north-south axis, the direction of prevailing winds.

Males on the alluvium disperse significantly more pollen than males on the slope (table 1). Males growing on the alluvium dispersed significantly more pollen than hermaphrodites on the alluvium. Hermaphrodites on the alluvium dispersed significantly more pollen than hermaphrodites on the slope. Since statistical analysis allows only three orthogonal contrasts, we cannot directly test whether or not males on the slope disperse more pollen than hermaphrodites on the slope. However, since males on the slope dispersed more pollen than hermaphrodites on the alluvium, and since hermaphrodites on the alluvium dispersed significantly more pollen than those on the slope, it seems safe to conclude that hermaphrodites on the

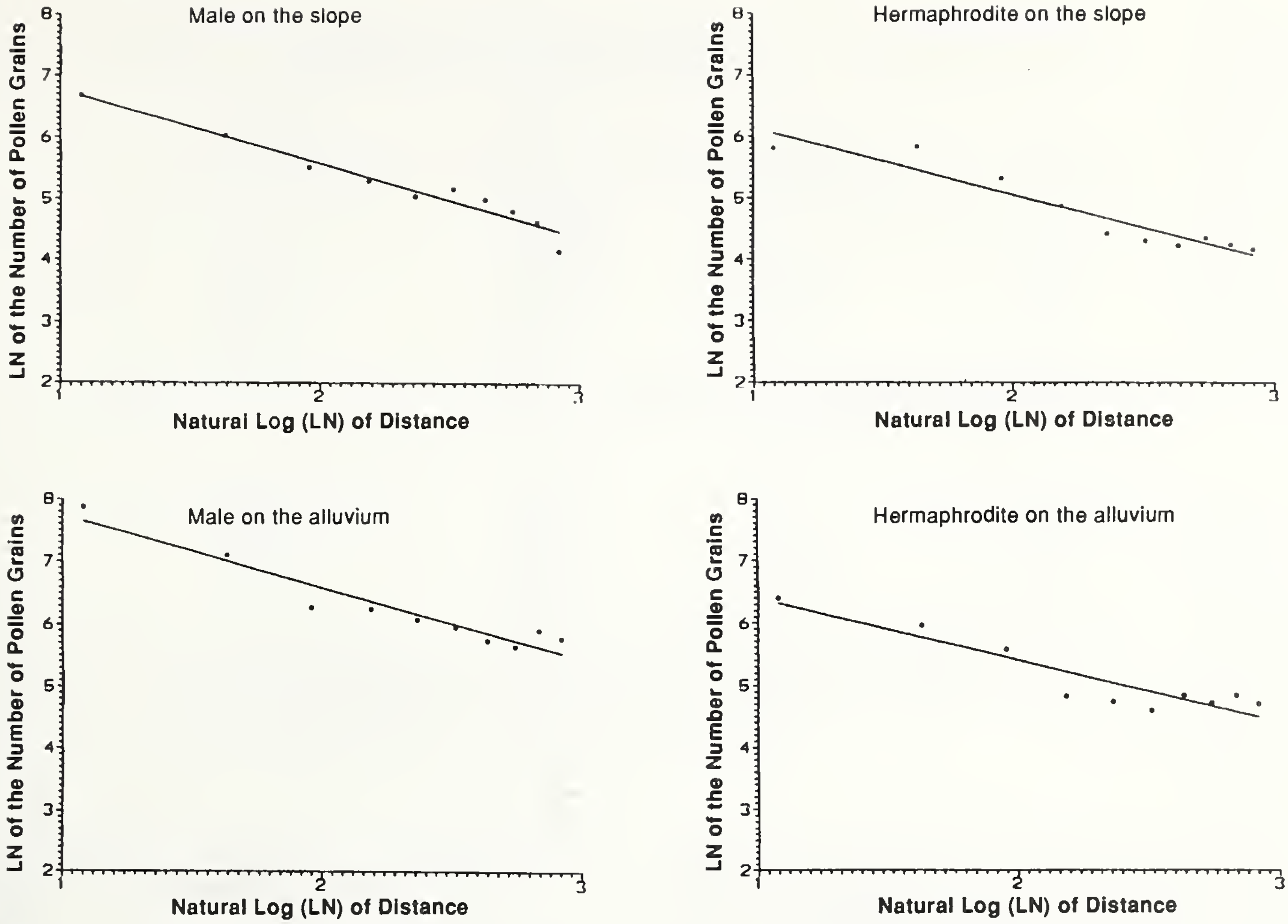

Figure 2—Dispersal of pollen to the north.

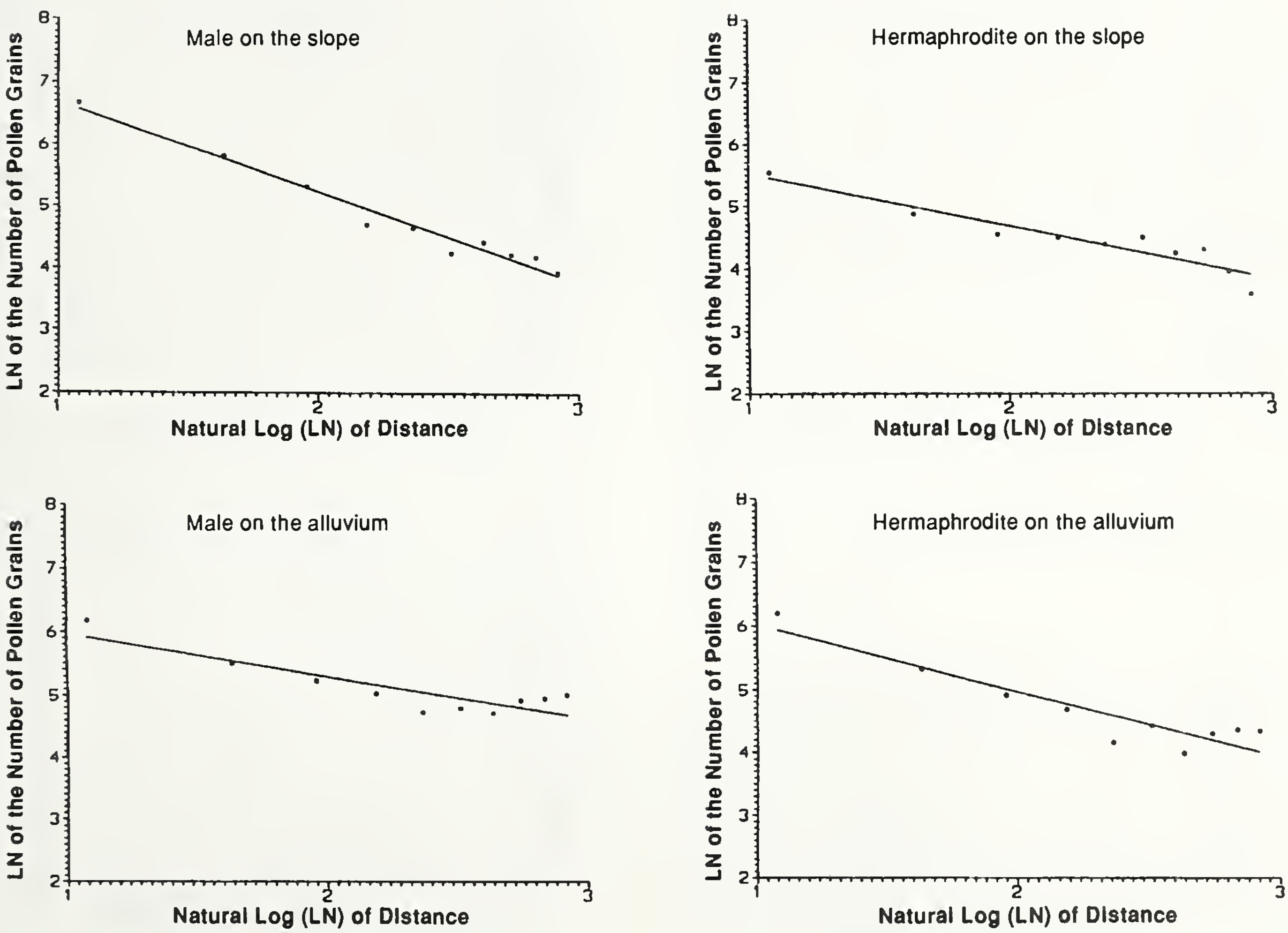

Figure 3—Dispersal of pollen to the east.

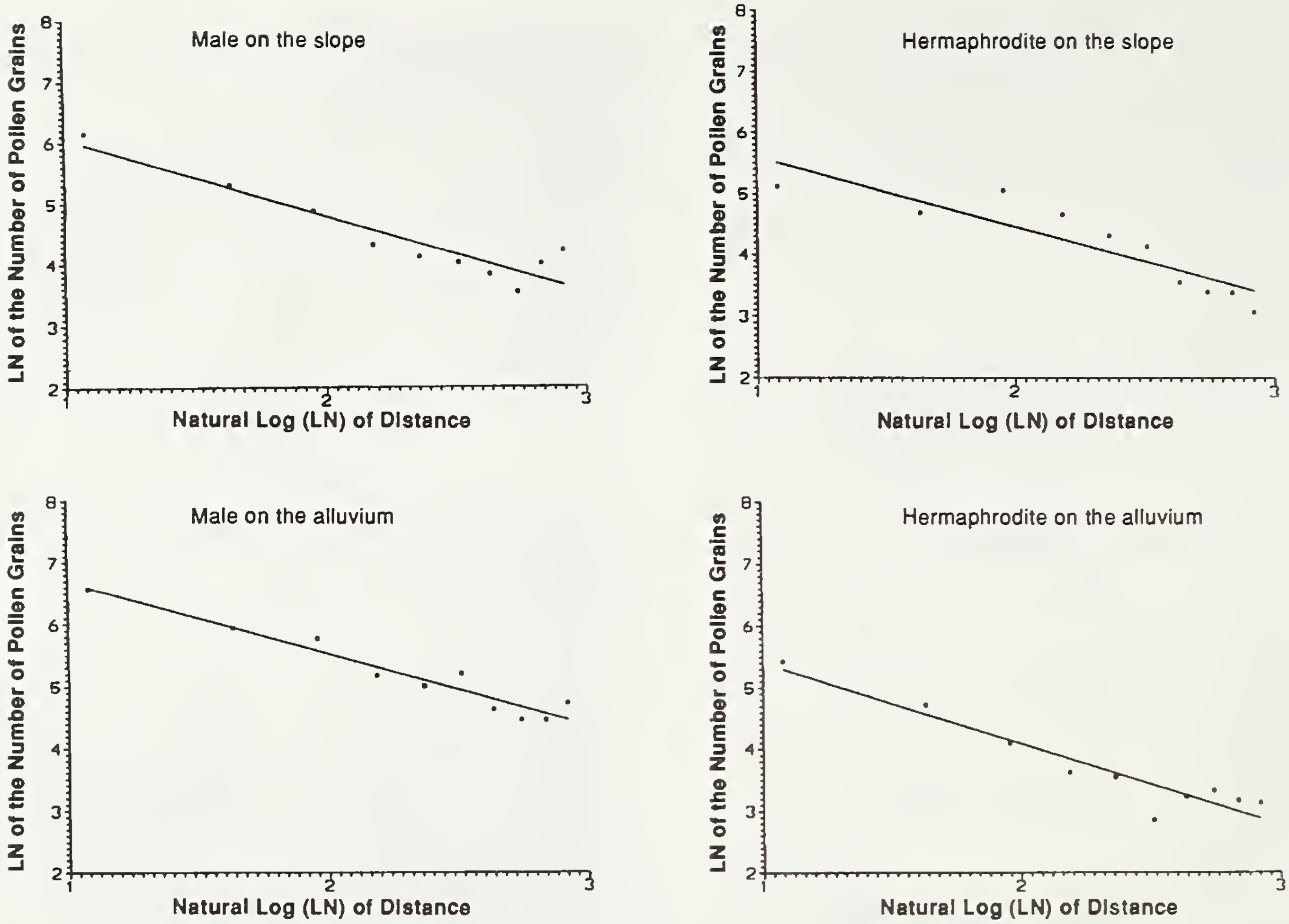

Figure 4—Dispersal of pollen to the south.

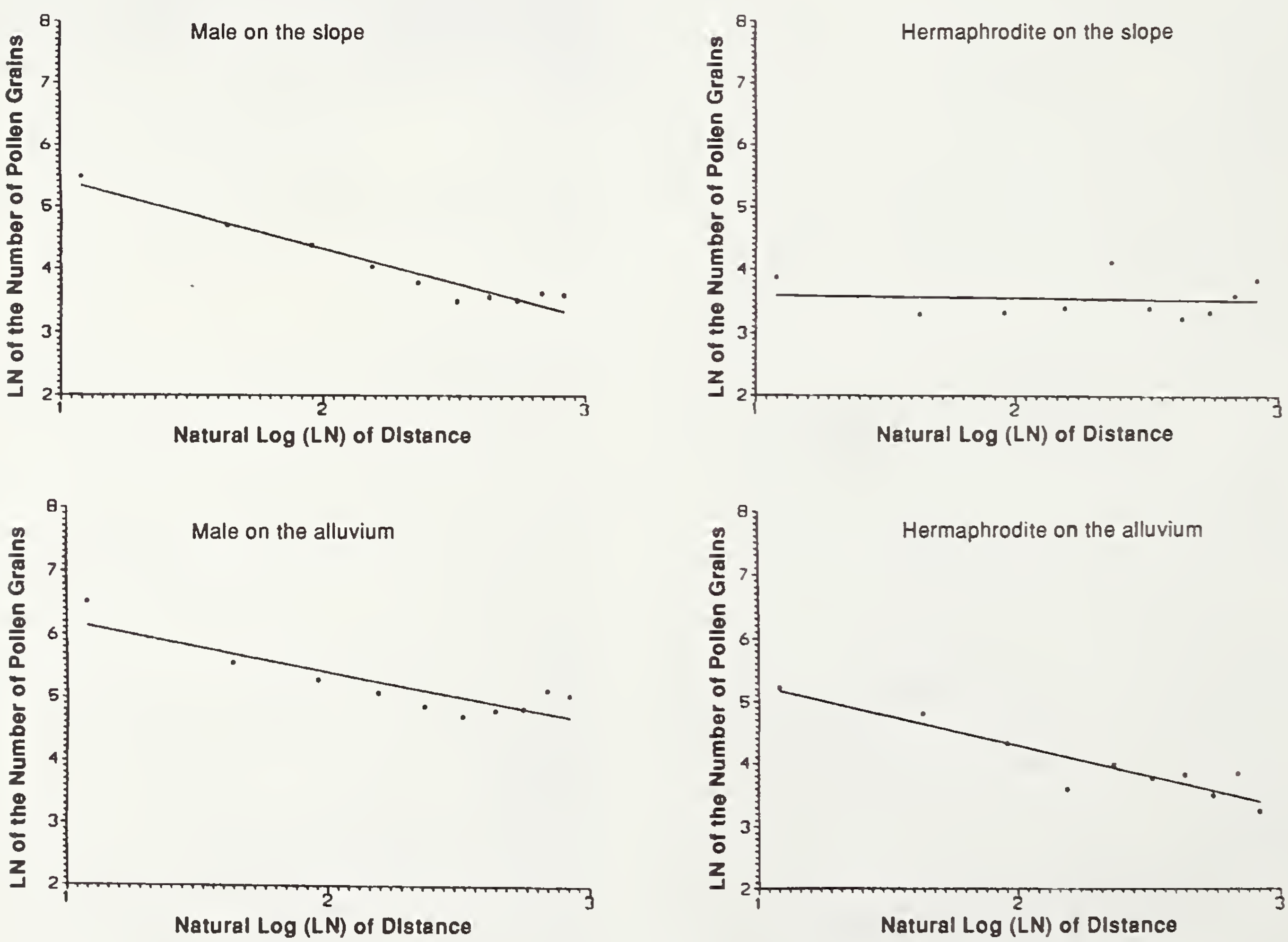

Figure 5—Dispersal of pollen to the west.

Table 1—Values for *t* for orthogonal contrasts of pollen dispersal for fourwing saltbush males and hermaphrodites

Direction of pollen dispersal	Pollen volume contrasts[1]		
	AM vs. SM	*AM vs. AH*	*AH vs. SH*
North	2.75*[2]	7.27*	2.05*
East	2.10*	9.52*	4.56*
South	3.27*	9.09*	2.73*
West	3.45*	.02	2.46*
	Pollen grains per unit of plant volume contrasts[1]		
	SM vs. AM	*AM vs. AH*	*AH vs. SH*
North	22.89*	5.87*	4.69*
East	18.48*	3.37*	4.41*
South	22.61*	6.02*	5.02*
West	24.79*	5.89*	5.97*

[1]AM = males on the alluvium, SM = males on the slope, AH = hermaphrodites on the alluvium, and SH = hermaphrodites on the slope. In each contrast the class with the highest value is listed first.
[2]* = $P < 0.05$, based on *t* test, 216 degrees of freedom.

slope disperse significantly less pollen than males on the slope.

These data were not corrected for the size of the donor plant, however. Such a correction dramatically alters the results. For each direction, males on the slope dispersed the most pollen grains per unit of plant volume (figs. 6 to 10). Males on the slope dispersed significantly more pollen per unit of plant volume than did males on the alluvium (table 1). Males on the alluvium dispersed significantly more pollen per unit of plant volume than hermaphrodites on the alluvium. Hermaphrodites on the slope dispersed significantly fewer grains per unit of plant volume than hermaphrodites on the alluvium. We conclude that males on the slope disperse significantly more pollen per unit of plant volume than do hermaphrodites on the slope.

If plants became more efficient at dispersing pollen as they grew, then we would expect a positive correlation between the number of dispersed pollen grains per unit of plant volume and the volume of the plant. A negative correlation would be expected if plants became less efficient at dispersing pollen as they grew. We regressed the number of dispersed pollen grains per unit of plant volume on both the volume of the donor plant and the pollen trap's distance from the donor plant (see fig. 10 for an example). The distance term was forced to enter the regression equation before the volume term, deliberately underestimating the influence of volume. In 10 of the 16 possible cases, the correlation between the number of dispersed pollen grains and plant volume was significantly ($P \leq 0.05$) negative (table 2). In one case—males on the alluvium dispersing pollen to the north—the correlation was significantly ($P = 0.05$) positive. The other five cases were not significant. In four of the five nonsignificant cases, the correlation was negative. In the case of pollen dispersing to the north for hermaphrodites on the alluvium and on the slope, the probabilities were 0.10, approaching statistical significance.

A plant's surface area-to-volume ratio probably affects the efficiency of pollen dispersal. While the production of pollen is likely related to plant volume, the release of pollen depends upon the surface area in contact with the wind. We regressed the number of dispersed pollen grains per unit of plant volume against the plant's surface area-to-volume ratio. Not surprisingly, we found that the correlation was significantly ($P \leq 0.05$) positive for nine of the 10 cases in which there was a significant ($P \leq 0.05$) negative correlation between the number of dispersed pollen grains and plant volume. Surface area was negatively correlated with dispersed pollen in one case (that of pollen dispersing to the south for males on the alluvium) and nonsignificant in five cases (table 2).

DISCUSSION

It has been suggested that differences in the utilization of common resources by males and females are due to differences in the costs and mechanics of reproduction (Charnov and Dawson 1989; Freeman and McArthur 1982; Freeman and others 1976; Freeman and Vitale 1985; Meagher 1980). We have shown that the dispersal of pollen can be influenced by the size, topographic position, and gender of the plant. Topographic position also significantly affects the

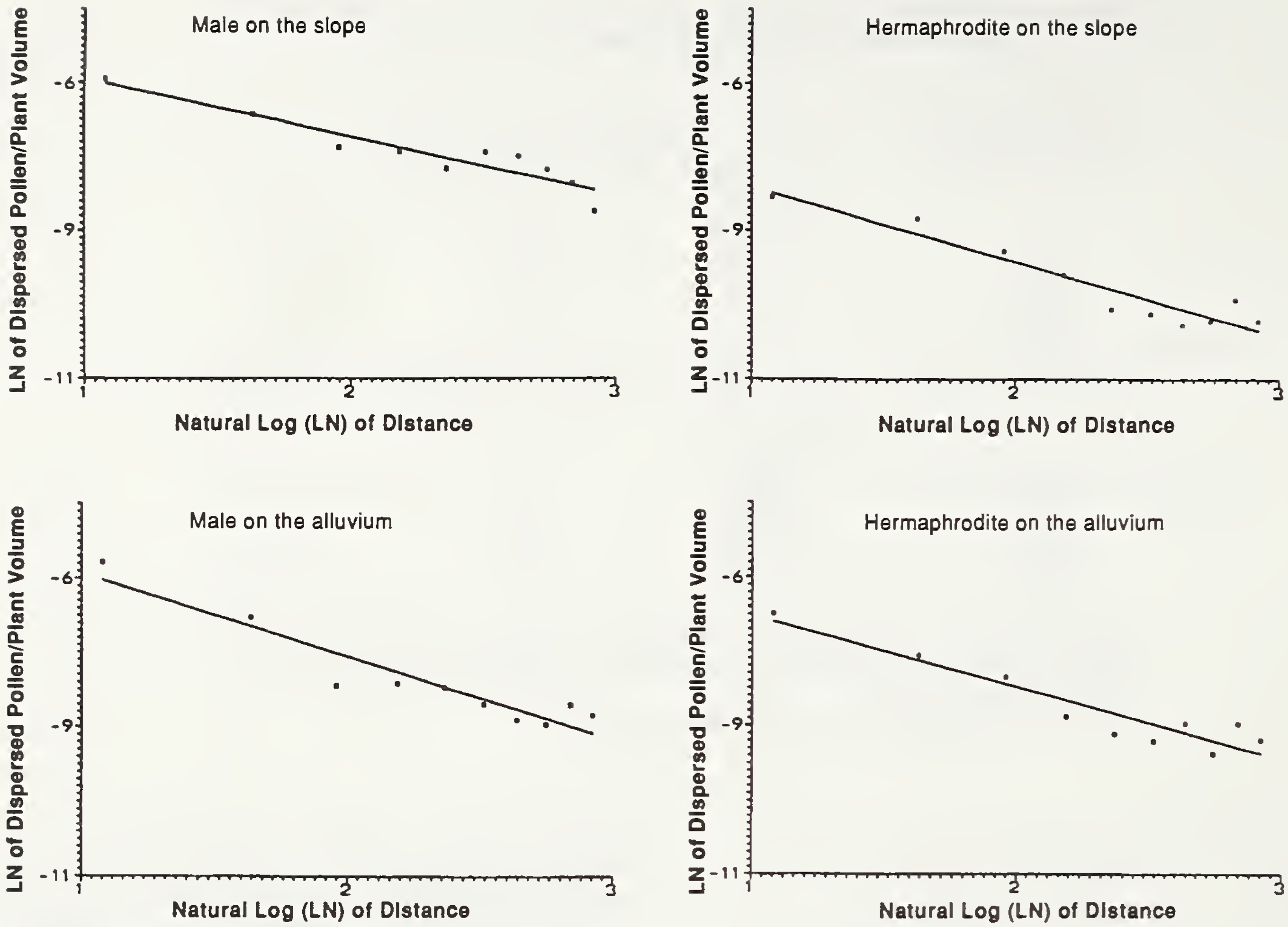

Figure 6—Pollen grains/unit plant volume dispersed to the north.

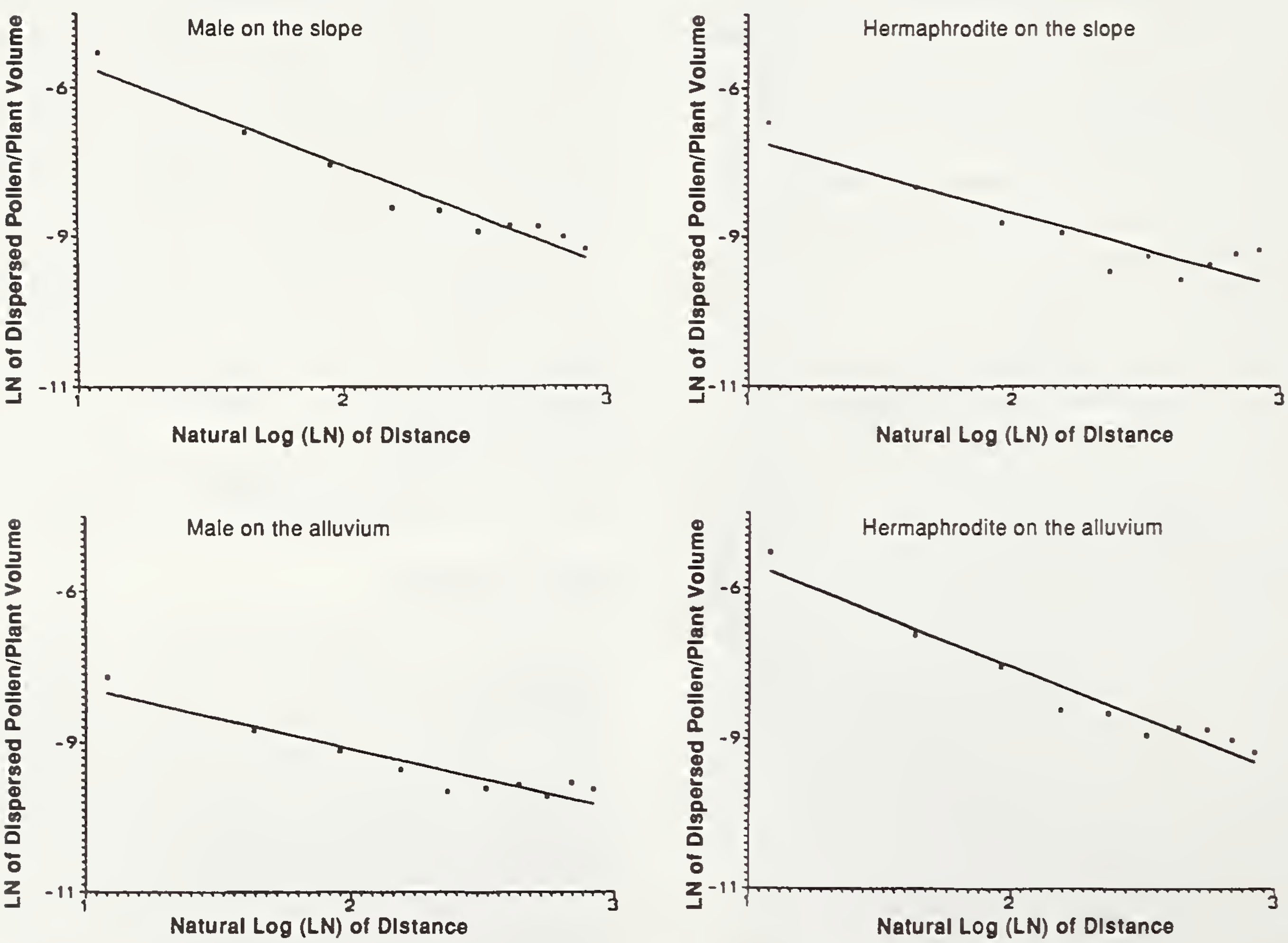

Figure 7—Pollen grains/unit plant volume dispersed to the east.

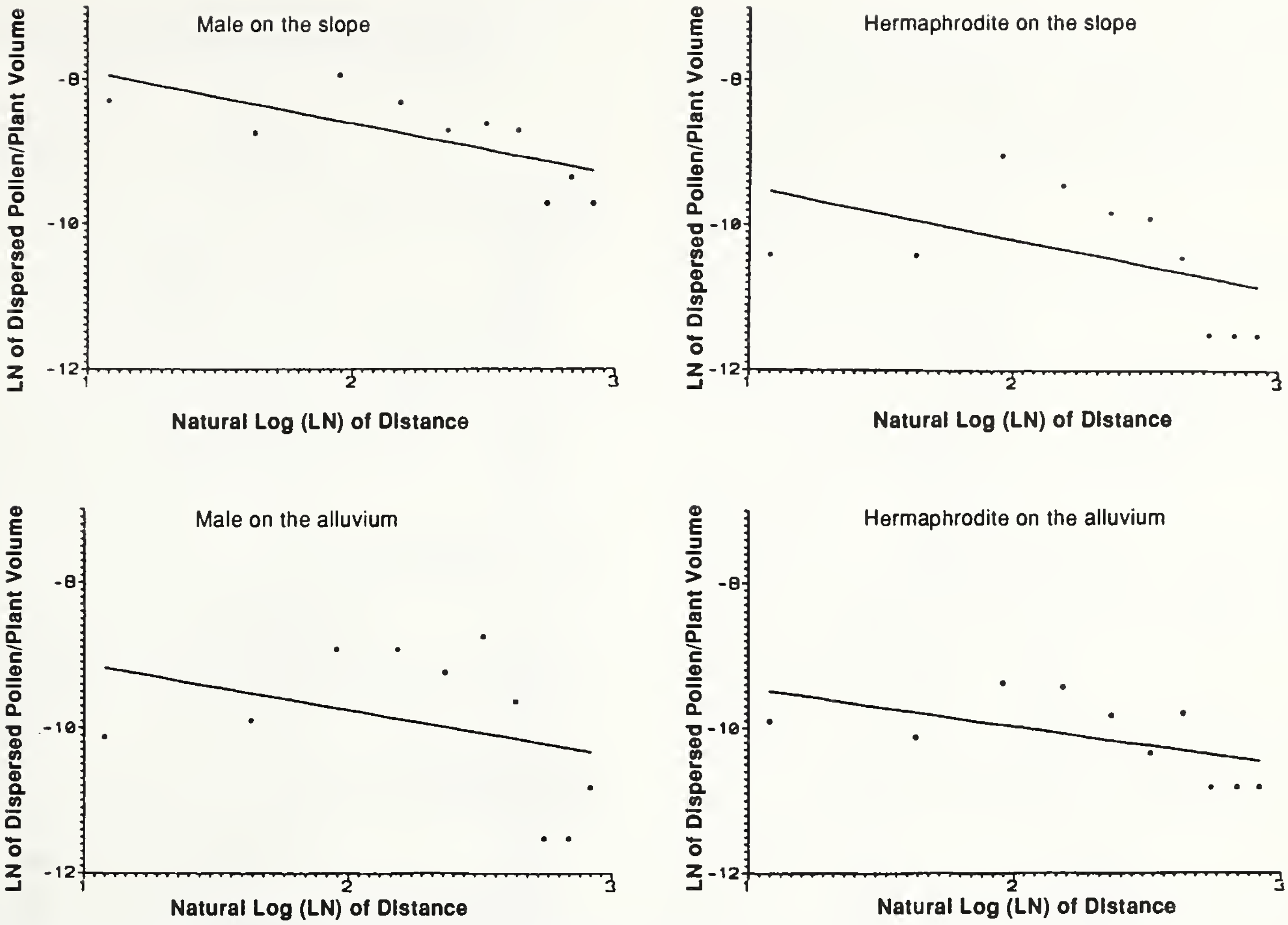

Figure 8—Pollen grains/unit plant volume dispersed to the south.

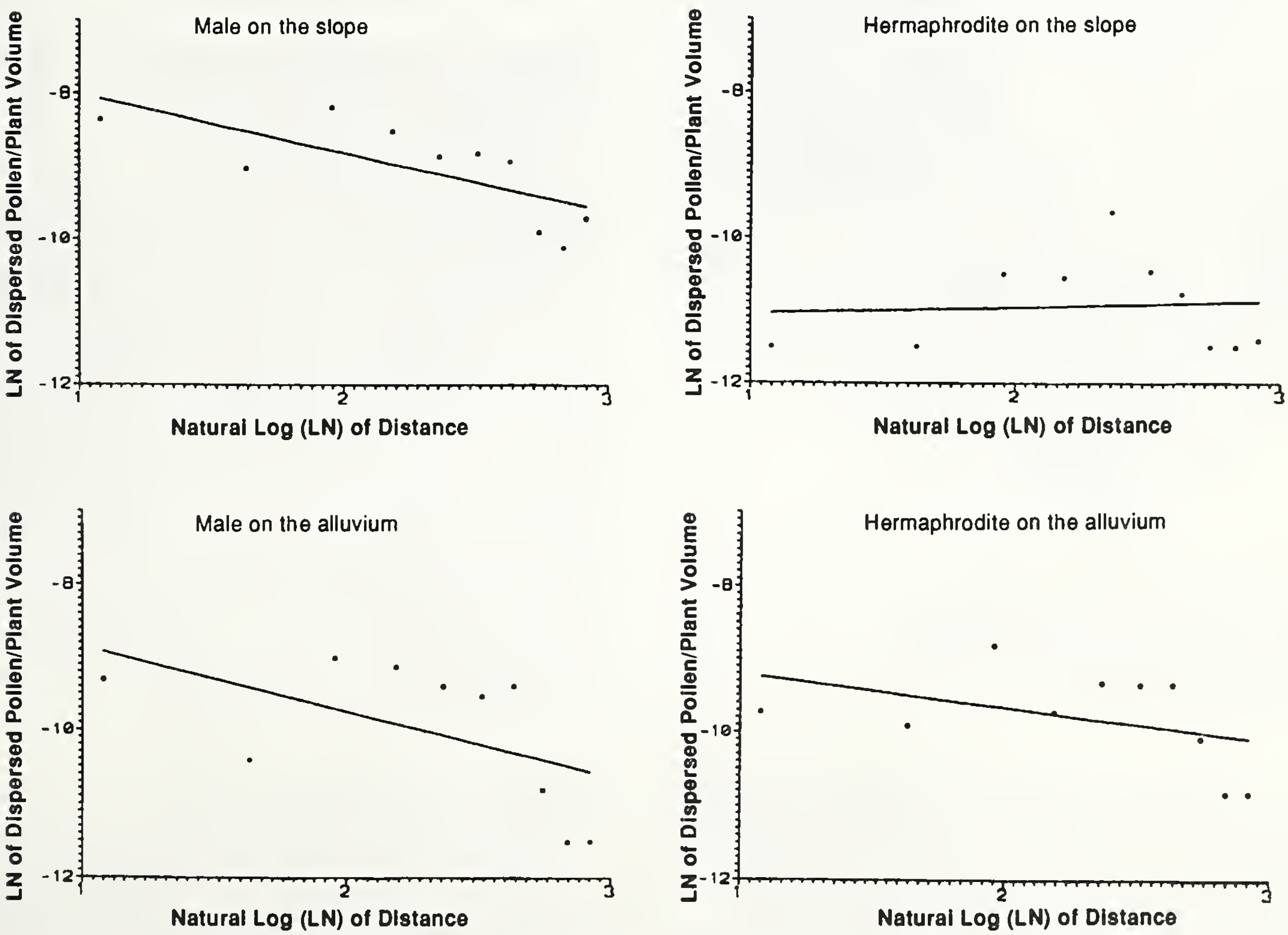

Figure 9—Pollen grains/unit plant volume dispersed to the west.

Table 2—The influence of increasing size on pollen dispersal and fruit production considered for both volume and surface-to-volume ratio

	Volume		Surface/volume	
	Partial *R*	*P*	Partial *R*	*P*
Males on the alluvium				
North	0.222	0.05	0.237	0.05
East	–.442	.001	.322	.005
South	.011	NS[1]	–.135	NS
West	–.121	NS	([2])	([2])
Males on the slope				
North	–.456	.0001	.609	.001
East	–.210	.05	.203	NS
South	–.231	.05	.401	.001
West	–.457	.001	.371	.001
Hermaphrodites on the alluvium				
North	–.282	NS	.228	NS
East	–.375	.01	.555	.001
South	–.338	.05	.359	.025
West	–.431	.025	.238	NS
Hermaphrodites on the slope				
North	–.273	NS	.170	NS
East	–.444	.001	.660	.0001
South	–.442	.005	.376	.01
West	–.074	NS	.518	.0006

[1]NS = not significant at the $P < 0.05$ level.
[2]F was insufficient for computation.

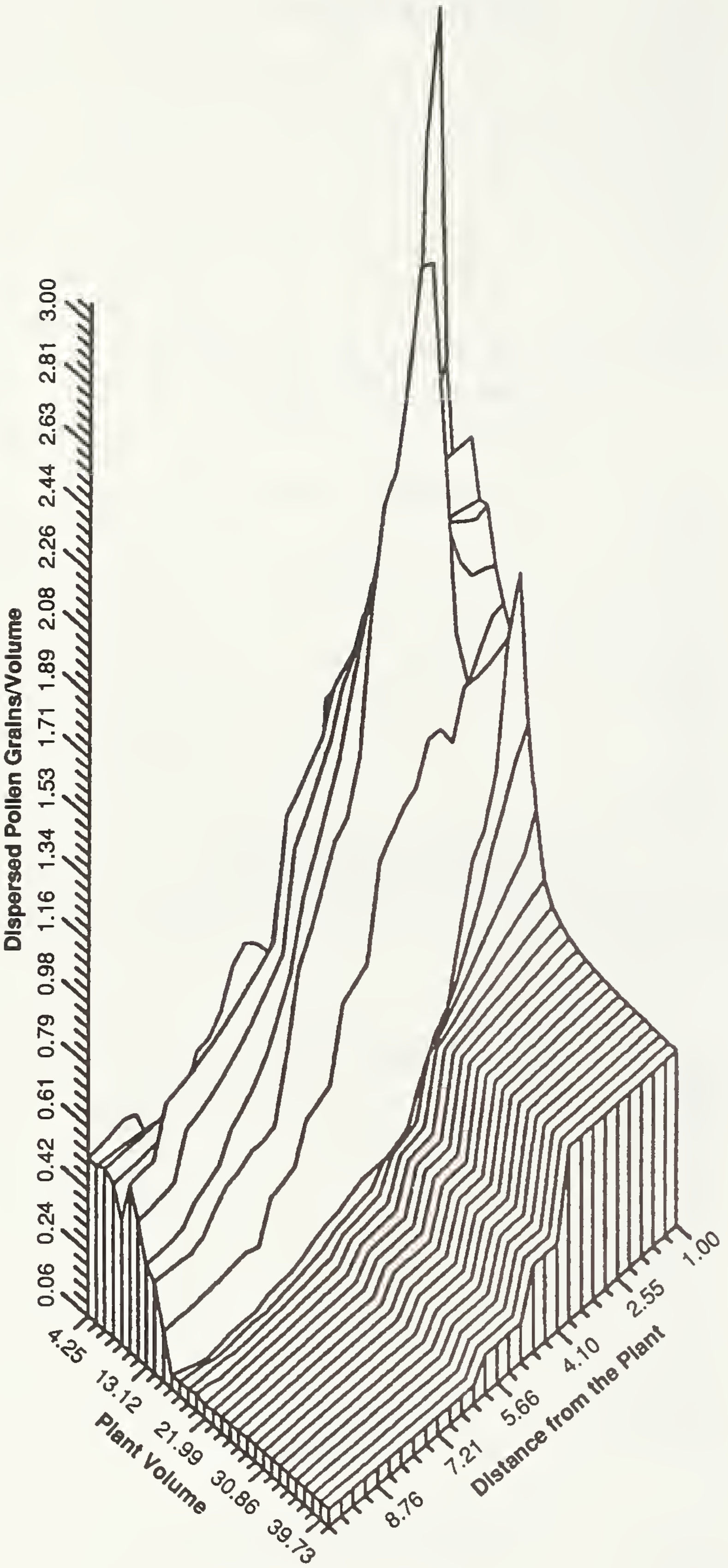

Figure 10—Dispersed pollen grains per unit plant volume as a function of distance (meters) and plant volume (liters). Data are for slope hermaphrodites.

efficiency with which plants disperse pollen. Males growing on the alluvium disperse significantly more pollen than males on the slope (figs. 2 to 5). But when we divided the number of pollen grains dispersed a given distance by the size of the donor plant, males on the slope were found to be considerably more efficient at dispersing pollen than males growing on the alluvium (figs. 6 to 9).

Our data show that the number of pollen grains dispersed per unit of plant volume actually declines as the size of the donor plant increases (table 2 and fig. 10). Pollen dispersed per unit volume is positively correlated with the plant's surface-to-volume ratio, but negatively correlated with its volume. Since males on the slope are smaller than those on the alluvium, they disperse pollen more efficiently. Windspeeds are probably higher on the slope, enhancing dispersal. The data presented here, together with that of Freeman and others (1993), demonstrate differential reproductive fitness among the female (pistillate), male (staminate), and hermaphroditic (monoecious) genders of fourwing saltbush. These data provide empirical support for maintenance of the trioecious breeding system of fourwing saltbush.

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